PRESENT THEORIES OF EVOLUTION AND THE PROBLEM OF ADAPTATION

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The Joseph Leidy Memorial Lecture
in Science

The University of Pennsylvania
Philadelphia
1933

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The history of biology even for short periods shows, among other things, how much the point of view is changing, though the main problems, under different aspects, really remain the same. This is the universal experience of men of my own generation who about forty years ago entered scientific life. Most of the theories of general biology which were in great favor and seemed to be the definitive expression of truth at the time of our youth are now in the background; so, for instance, the idea of phylogenetic trees and the law of recapitulation, which seemed then the center of every evolutionary considerations. We could hardly find among the teachings or original works of today any notable discussion of these topics. Many hypotheses which seemed evident are now doubtful or even completely rejected. The progress of knowledge has deeply modified the relations of things as they appeared; but, as in many human activities, progress is not alone responsible for that, for there are, even in habits of thinking, fashions which leads the minds of workers in certain directions. Forty years ago we were in the age of phylogeny. I would be inclined to say that we are now in the age of chromosomes.

As a consequence, many of the principal problems of biology appear in quite different relations. Thus in the case of adaptation, which I believe may be termed the key problem of evolution. I would like to try to examine how this is really related to theories and facts at present in favor.

Adaptation is the harmony between the anatomical structure and functions of living organisms and environmental conditions. Two main questions arise concerning it: first, is adaptation a fact; and, second, how was

adaptation effected. Both problems in modern biology were prominent in the minds of the greatest naturalists, however much opposed were their views, as in the case of Cuvier and Lamarck, Buffon and Charles Darwin. Adaptation was really the nodal point of all their meditations and they proposed very diverse solutions to explain it. Today adaptation is still the sensitive point of biology. Opinions are divergent as to the extent, even as to the very reality, of adaptation. The chief difficulty is to know how adaptation could be effected, taking into account our present knowledge, both by way of observation and experimentation, in the fields of development and differentiation of organisms, and in that of heredity.

I do not intend at all to attempt here the solution of this great and difficult problem, but it seems of interest to confront it with the present ideas, to analyze its principal elements, and simply to realize its difficulties.

If we consider first the fact of adaptation there are two different aspects—*internal* and *external* adaptation. Internal adaptation is the harmony and solidarity between the different parts and organs of an organism; external adaptation is the conformity of special parts, or of the whole, to environmental conditions and habits of life. Organisms appear to be generally more or less moulded, both internally and externally, by their environment.

It will be convenient to recall briefly what are the principal indications of such a general conformity. We can put first the traditional and oldest conception, that of general finality in Nature, initiated by Providential design. Such is the understanding of Réaumur, of Bernardin de St. Pierre, and of Cuvier. Science is, above all, the contemplation and discovery of the harmony of Nature as irrevocably ruled by Providence. Adaptation is thus a universal and *a priori* condition of the structure of organisms, the manifestation of the conception of Providence organizing all the world. It really is a plan,

both general and particular, of the relations of the organism to other organisms and to the environment. Each kind of organism has, in the universe as a whole, a special and fixed part to play, and has received the appropriate organs to do it. The various parts of the organism are correlated with this end in view. It is the aim of Science to analyze them and to rebuild the plan of Nature as ruled by the Creator. Cuvier thus came to an understanding of his two great principles of animal organization:—that of organic correlations, and that of conditions of existence. Such were the foundations on which he succeeded, a little more than a century ago, in discovering and ordering many of the most important facts of comparative anatomy. Adaptation was for him a universal property of living matter. "It is not enough for the persistence of the world," he says, "that the parts of each organism be in mutual harmony, which is the necessary condition of existence, but organisms must be in the same harmony among themselves. Various species are essentially needed—some as prey, others as destroyers and moderators of propagation. It would be impossible rationally to conceive a situation where there would be flies without swallows, and conversely. . ."

The connection between general natural facts, as Cuvier formulates it, is a matter of contest. However, in Cuvier's conception the foresight of Providence must be extended to every minute detail of creation. Adaptation must be a universal property of living things, discoverable everywhere by adequate analysis.

We cannot any longer subscribe to such a conception and it is easy to condemn Cuvier for it. Yet Cuvier remains one of the greatest geniuses in biology and, despite the unsoundness of his primary conception, he succeeded in discovering and in ordering an enormous number of facts, thus founding both comparative anatomy and paleontology.

Quite contrary is the conception of adaptation of Lamarck, for to him it is not at all a question of *a priori*

established harmony in organisms and between them and the environment. Adaptation is just as real and universal as for Cuvier, but it is an *a posteriori* fact. That is, it results from the action of the environment on the organism. Environment moulds the organism, which is always responding to external stimuli by changing according to them, and by finally adapting itself to them. Environment induces needs, needs induce habits, and so use or disuse of organs. Useful organs are thus improving themselves, differentiating, while useless ones are becoming reduced, until they finally disappear. Function creates organs. Such is the direct effect on the organs of the individual; this process, acting on young and developing individuals is transmitted to the subsequent generations by heredity of acquired habits and characters. Herein is the summary of the Lamarckian doctrine, the first formulation of an entire and consistent evolutionary theory. As to the proofs of it one may say that they are extremely poor and were difficult to find at the beginning of the last century. The doctrine is much more one of intuition than of real demonstration. The weakness of the proofs was evident to Cuvier and was severely criticized by him. So the Lamarckian theory fell.

It should be recalled that, while more prudent in many respects, the conceptions of Geoffroy St. Hilaire were no less audacious. He recognized, for instance, in Vertebrates the necessity for respiration when passing from water to air as the powerful agent of transformation from fish or amphibian organization to reptilian.

The essential characteristics of the Lamarckian doctrine and of all subsequent modifications of it rest in the direct influence of the environment on changes in organisms. Environmental factors are the primary factors in evolution and was indicated by the eminent French biologist, Alfred Giard. Adaptation appears, even to the biologist of today, as a general or universal characteristic of all biological organization.

A third point of view whose ultimate consequence is about the same is that of Charles Darwin, who, as is well known, did not consider the origin and source of variations, but, given variations, analyzes the manner in which they are later perpetuated or eliminated. Everyone knows perfectly the mechanism of natural selection, resulting in the survival of the fittest. Fitness is thus the general characteristic of existing organisms, so that adaptation remains here also a general, if not universal, property. It must be remarked, however, that apparently at least fitness or adaptation in the Darwinian sense does not rest upon primary finality. The special merit of Darwin's view, it has frequently been emphasized, is in the elimination of finality in the understanding of biological organization. But how can fitness be discerned? What is the objective criterion of utility of a given variation? In most cases it is the fact that such a variation has persisted. As a matter of fact, the Darwinian doctrine is not as independent of the concept of finality as is generally believed. It is not our place here to discuss this point. My aim is merely to indicate the relation of the idea of adaptation to the doctrine itself.

The three conceptions just stated have in common the universality of adaptation. In those which I am about to discuss, this is not the case, for adaptation is considered as a fact but partially applicable, or even that it should be entirely excluded. In a general way these conceptions are the modern ones.

First we have to mention the theory of *preadaptation* as formulated by Cuenot. Adaptation is no longer a universal property, an *a priori* fact, as for Cuvier, nor a general *a posteriori* result, as for Lamarck and Darwin. Variations are produced independently of any consideration of utility, but once existing they are in fact compatible in whole or in part, or not at all, with the existence of each organism under given conditions. Confronted with the struggle for life the bearer of new structures persists when it can find in Nature places both

convenient and lacking fatal competition by organisms that are better equipped—what Cuenot calls *empty places*. These new forms are, in fact, fully adapted. Adaptation does not result in active modifications of the organism in order to be in harmony with the environment, but in the haphazard correspondence of the organism to a given set of conditions in an independently existing environment. This does not necessarily mean that the entire organism is adapted. Many arrangements are even more or less unfavorable. The organism does not acquire the structures adapted to the environment; it is compelled to choose an environment and habits of life compatible with its own organization. This was very skillfully developed by Cuénot, but such views are really not quite new in Science. We find them expressed by Buffon. Studying the habits of the woodpecker—a favorite example for many naturalists, and particularly for Darwin, Buffon writes: "He received from Nature organs and instruments fitted to his mode of life, to his destiny; or, rather, this destiny results from the organs he was born with." Buffon, and Darwin after him, have particularly well explained, for instance, how well adapted the tongue of the woodpecker is to the catching of insects in the holes of the wood, one of the most striking examples of adaptation. This, however, was later considered by Darwin to be the effect of natural selection. And we realize in this case how the same facts can be interpreted in very different ways.

In these latter conceptions, adaptation comes to be completely denied by certain modern naturalists, as for instance my colleague Etienne Rabaud of Paris, in a book "Adaptation and Evolution" published about ten years ago. Adaptation for him is purely illusive, not a reality. Yet some or many organs show more or less harmony with the environmental conditions of life, but there are no relations at all of cause to effect between them. Anatomical structures are quite independently produced from functions, and have no adaptative mean-

ing at all. The only true adaptation is of physiological order. A given environment forces the organism to a given system of exchanges and metabolism, the completion of which is the absolute condition of persistence or of death. Animals and plants must accommodate themselves with the organs they have and with the structure of these organs. The structures, by themselves, have no relation at all to the conditions of life. Every appearance of real morphological adaptation is delusive. For instance, a classical case is the webbed structure of the feet of aquatic birds (Palmipeds). But there are birds of aquatic habit without interdigital membranes, such as the moor-hen (Gallinula chloropus), and on the other hand, there are some terrestrial birds with more or less palmate feet. Similar arguments are used for different examples such as blind or colorless animals living in the same conditions as those colored and with eyes; or it is attempted to show that organs of a perfectly instrumental nature, such as claws, or the grasping structures of the first pair of legs of Mantis, do not really play any essential part in the life habits of the animals possessing them. In the same way, under the same conditions of life, as in the case of fishes in water, there are quite divergent forms of the body; and aquatic animals, such as the Salamanders, do not use the interdigital palmation of the digits as an oar to propel themselves in water, but keep the limb always close to the body in swimming—and so on. To sum up, morphological adaptation has no reality but is simple illusion.

Such are the principal beliefs concerning adaptation and its more or less general ramifications. They are far from being universal and, before going farther, it is necessary to compare them.

It seems to me that reality, and even a great extension of really adaptative structures, cannot be denied without refuting every evolutionary conception, and before an audience of naturalists such as this, it seems to

me not necessary to discuss this point exhaustively. Here, as in every similar problem, the positive facts are the most conclusive. In reality they are the only ones to be conclusive. On negative facts one can hardly build anything firm.

If we agree that the birds come from reptilian ancestors, how could it be denied that the whole of the structure of the avian body, and especially the structure of certain organs of it, are evidence of adaptative transformations of those of the Reptiles? Examples of this are the structure and connections of the skeleton, the structure of the wings and of their musculature, the presence of feathers instead of scales, the modifications of the lungs, etc. . . .

No less impressive is the structure of aquatic mammals, and chiefly of the marine groups such as the Sirenians and Cetaceans. The general fish-like shape of the body, the complete reduction of hairs, the structure and reduction in number of limbs, the development of the tail in a powerful caudal fin, the differentiation in many cases of a dorsal fin, the structure of the skin with a thick fatty bed, and many anatomical modifications, making the Cetacean like a fish, cannot be reasonably understood without adaptation from a terrestrial mammalian ancestor.

It is the same with many Invertebrates—for instance the Pagurid Crustaceans, whose abdomen is evidently modified by adaptation to the life of the animal in empty Gastropod shells. All facts of this kind become much more impressible by their close parallelism in quite different groups under the same habit of life. *Convergence,* so-called, is, more than any other consideration, an unmistakable proof of adaptation; for instance, Cetacean and Sirenian and fossil marine Reptiles, such as the Ichthyosaurus; the common transparency of the body of quite different pelagic organisms, etc. It seems to me that it is no longer necessary to demonstrate the truth of the fact of adaptation. And it is not at all a con-

clusive fact against it that its effects are not always exactly the same and that in certain forms of animals of a given habit of life some peculiarity is missing, such as the interdigital membrane in the moor-hen. First, the conditions of life of different species of the same general habits and environment are not, and have not been, exactly the same; and, chiefly, each organism reacts as a whole and by its own correlations. Therefore the final results may be very different. Morphological dispositions, even the most impressive, are very indirectly and roughly connected with the essential working conditions of the organ and of the whole organism. Many compensations can interfere, in different shapes, between more or less related animals. We no longer rely upon such simple conditions of anatomical transformations as Lamarck thought possible. It can no longer be even a question of direct adaptative change of organs. The truth is that, if the organism as a whole is becoming modified by the environment, it reacts as a closed system of intrinsic correlated parts and so every anatomical modification cannot be adaptive. In the Cetacean, as in the bird, many anatomical peculiarities are not of directly adaptative nature, but the result of correlated modifications of others.

It is no longer conceivable that given conditions of life resulted in but one type of modification. It is not at all surprising that various organisms under the same general conditions show very variable or different modifications of structure, as in the example given of the feet of aquatic birds. However, in biology, as in every branch of science today, we are confronted with the idea that no law has an absolute and uniform value. The laws are the common resultant of a large set of particular facts not identical, but statistically compensatory. That is the case at present for most of the laws of physics, which are of purely statistical character. Many adaptations, as Cuenot has clearly formulated, are of statistical aspect. So the palmate structure of the feet of aquatic

birds, in spite of some exceptions in both directions, is clearly correlated with the aquatic mode of life. It is not likely that pure chance had resulted in such a statistical uniformity of conformation.

Truly the physiological aspect of adaptation must be, and really is, of much greater precision than the morphological one. And, as far as our knowledge goes, we find quite impressive examples of delicate and precise adaptative mechanisms in physiology. Claude Bernard was quite correct in insisting on the constancy of the internal environment of the cells and organs in higher groups of animals. We discover more and more delicate compensatory mechanisms for physiological regulations and without any doubt many are still to be discovered. So, for instance, Claude Bernard instanced the rôle of the sympathetic nervous system in regulating the circulation of the blood by constricting or enlarging the diameter of the blood vessels. I was personally much impressed two years ago at a general meeting of the Société de Biologie in Paris by the discussion of the structure and function of the nervous centers of the so-called carotid sinus—the nerve of Hering and the ganglia lying at the bifurcation of each carotid artery, by which is certainly regulated the pressure of the blood in the circulation. However, the functioning of every nervous center is of the same kind. Quite as impressive, and perhaps even more so, are the many and important recent discoveries in the field of endocrinology. But finally, such physiological regulations rest on anatomical structures, microscopical and practically impossible of analysis and description, but nevertheless real and truly of anatomical nature. One cannot make an absolute distinction and contradiction between anatomical and physiological adaptation. Physiological adaptations rest finally on anatomy.

We are therefore coming to admit the real truth of adaptation and particularly of morphological adaptation—not, however, as a universal property of the

organs whose structure must be a final compromise between the intrinsic correlations of the various parts of the organism and the effect of the environmental factors.

The problem is now—and it is of the greatest difficulty and far from being solved—to ascertain how adaptation could be made effective, how it comes to be a reality. There would be certainly no difficulty at all if we admitted the intervention of Almighty Providence as did Cuvier, but we must search only on the basis of action of the natural environmental factors on the organism. We must distinguish now two lines of inquiry—first, the realization of the individual organism in its ontogenetic development, and, second, on the basis of evolutionary conceptions, the gradual formation of the type. The first point of view is accessible to direct observation and to experimental analysis; the second, unfortunately, rests mainly on theoretical and hypothetical considerations. The data from the first are consequently of primary importance, but we cannot exclude the other.

Lamarck, a century ago, could know practically nothing about embryological development. We are, fortunately, in a quite different situation. Latterly we have acquired a very good knowledge, not only of the successive phases of the development of various groups of animals, but we can analyze, by direct experimentation, many of the essential conditions of developmental differentiation of the parts of organisms and of their relations to one another.

Without going into details, it seems to me that the principal results of our embryological knowledge is that the embryo, to a very large extent, is a self-differentiating system as a whole, even that the same is true for its different parts at successive stages of development. More and more the internal substratum of differentiation appears to exist from the beginning. So, for instance, we must abandon more and more the conception of an initial isotropy of the egg, and, on the contrary, adopt that of anisotropy where, though the future parts are

not performed, they are to a large extent predetermined. Quite recently the beautiful work of Conklin on the development of Amphioxus brought new and significant facts of such a nature. The organism differentiates itself by itself; the environmental circumstances do or do not permit development and differentiation of the parts, but have on them no directive action. They can induce, as we can determine by ingeniously conceived experimental interventions, more or less viable seriations of normal differentiation. From the egg to birth the organism performs a succession of changes perfectly regulated in advance by itself. And as far as the adaptative dispositions of parts are concerned they are, in individual development, completely realized before there is need of them; so for the molar teeth of the various groups of mammals, highly adaptive structures, such as Cuénot designated as coadaptative. These are really as precise, in view of a particular use, as are the instruments made for a definite purpose by the hand of man. I could easily consider here many such coadaptations. One of the most remarkable known to me is the system of two chitinous teeth articulated on each other, by which a Polychaete annelid, Ichthyotomus sanguinarius, parasitic on the fins of some marine eelfish, remarkably studied by Eisig, adheres to its host. This is a really precise instrument whose parts are completely differentiated before they are to be used. However, the structure and forms of embryos and larvae of most of the parasites during development confront us with such highly adaptive capacities for meeting the conditions which the parasite has to overcome. We do not find, therefore, generally, in the present understanding of individual development the key to the progressive formation of adaptive structures. Everything is definitely and precisely fixed from the beginning.

Now let us look at this evolutionary differentiation in the course of phylogeny, though unfortunately there is no possibility of observation or experimentation. It

appears evident that all the possible solutions rely finally on two groups, the Lamarckian and the non-Lamarckian. The Lamarckian concept is founded on some kind of heredity of acquired characters. But we know that every effort to demonstrate it in the last decade has failed. However, the very ingenious dialectics of Weismann in opposing soma and gene, and the subsequent progress of our knowledge of heredity by genetical methods, tend to suggest to us the theoretical impossibility of such a heredity of acquired characters. And it is no doubt that at present most biologists feel perfectly sure that it is an impossibility. But to fail to understand the way to realization of transmission from soma to germ is not a sufficient reason to deny entirely this possibility. On the other, non-Lamarckian, side we must apply to chance for producing the adaptative dispositions we find in present-day organisms, the conservation and accumulation of such modifications being controlled by natural selection.

As a matter of fact, we now come in touch with a large number of hereditary variations, accurately observed, and whose laws of transmission are perfectly clear, that is, mutations. They are sudden, more or less important, at every level, beginning with great discontinuity. Mutations are at present the facts whereby biologists realize the effectiveness of evolution in the past and its confirmation in the present.

I would not in any way contest the great and real value of the concept of mutations; it is evident from the precision of experimental work and the general and uniform character of their laws. We have gained through them the first solid knowledge of heredity and of hereditary variations. The general data of Genetics as they were acquired in the last thirty years and as they are progressing more and more each year, are certainly the most effective advances made in general biology, by far more solid than the phylogenetical speculations of the preceding period.

Mutations show nothing at all of an adaptive direc-

tion in the variation of species; they occur spontaneously as results of chance combinations of elementary parts or genes in the processes of meiosis and fertilization, producing variations without any relation to environmental conditions. We are now able to induce them by external agencies, such as X-rays, and even more simple and general agents such as heat. Recently Jllos succeeded in accumulating such effects in a given direction, suggesting orthogenesis, which is one of the dominant aspects of evolutionary facts. Taking everything into consideration, the production of mutations rests finally on chance and shows nothing in connection with adaptation. We must accept the facts as they are.

But the problem is, what is the real bearing of mutations on evolution? Many biologists of today, I know, impressed by the experimental facts, both positive, as for mutations, and negative, as in experiments on inheritance of acquired characters, conceive the entire evolutionary process as effected by successive mutations, under the control of natural selection.

As convincing as are the facts, they do not seem to me to have such an extensive significance. Mutations are the expression of possible combinations in the frame of the stabilized species. Most of them, however, can be perpetuated only under the experimenter's control and would disappear rapidly in the conditions of Nature. However, they certainly are frequently produced under natural conditions, but apparently are quickly eliminated. Many are pathological combinations and the progress of genetics itself shows how many are lethals. Certainly if many are bad some may be good, and there are some such examples such as tetraploidy. But, taking everything into consideration, it seems to me that such a process cannot be regarded as the way by which all evolution took place. They show the multiplicity of possible forms for a given species, they reveal the hereditary constitution of a given type, more than the formation of new independent types. They represent combinations of

existing things more than formation of really new things. We are confronted in Nature with different species and with variability in each of them. Genetics has brought us a much clearer notion of both. Mutations, up to the present, have been entirely intraspecific. They can, for certain structural characters, be more different from type than authentic different species are; yet their constitution and general properties are those of the original species. They seem to be one of the aspects of the stabilized standing of organisms rather than a bad evolutionary process. It would not, however, be denied that they can show us the way of diversification of species in a given group, such as a genus, which has nothing to do with adaptation. But evolution, as a whole, cannot be reduced to this step. The main problem is the constitution of larger types and groups. Is such an evolution a continuous, permanent and indefinite process? Is it still noticeably going on in Nature, or has it come practically to an end so that we can no longer observe true evolution as it takes place? This question can be put, but not precisely settled, and in the short time we have for making observations, we must have the illusion of stability even though change is really going on at the same rate as in geological times. But paleontological evidence is far from giving to us an idea of continuous and simultaneous change of all organisms. Each type seems to have had its own time of evolutionary rise and diversification, to be after that stabilized and to gradually disappear. When the era of Reptiles was over there came that of Mammals. Neither the Reptiles nor the Mammals are at present forming new types or differentiating themselves as formerly. It is quite possible that the conditions of a real evolution—that is, formation of new types—are now over, that most of the organisms are in a stable situation where environment is no more practically effective on their constitutions in the way of altering them substantially. The facts we witness could not, if so, show us how the real evolutionary changes which

moulded the type were effected and where environmental factors induced adaptative changes.

A few facts, however, can throw some light upon the whole question. One of the most striking groups of facts relates to the cave animals, many of which lost pigmentation, came to have reduced eyes, or are even entirely blind. A similar situation occurs for the abyssal animals. In both cases we are not confronted with uniformity; very different, even opposite, examples can be invoked and, on their basis, any adaptation is denied. The statistical aspect of things indicates certainly a direct connection between the life of the species in the dark and the reduction of pigmentation and vision. Experiments of the limited nature we are enabled to make give no positive results at all, but we must not be astonished by this. And certainly it cannot be a question in the present state of knowledge of any direct hereditary response to darkness. But some types living in darkness from more or less remote periods show at present an undeniable instability for pigmentation, or vision, which is very likely the sign of evolutionary changes still going on, where effective action, at least an indirect one, of environment in an adaptive sense cannot be reasonably denied.

Such is the case of Proteus sanguineus of the caves of Europe. The body is quite pale in darkness; but if kept in light, the pigmentation reappears; it is not really lost. One of the elements responsible for its production must be stimulated by light; but in other surface Salamanders pigmentation arises even in darkness. Something was lost by Proteus through life in the caves. Similarly the eyes, under normal conditions, after developing up to a certain stage, stop and differentiation retrogresses. Now Kammurer showed indisputably that young Proteus bred not in the dark, but in alternative white and red light, acquires much larger eyes of greater differentiation,—in fact almost normal ones. We find here a degree of instability of the differentiation of the eyes which can be interpreted only as an evolutionary

process of regression of the organ, and the relation to living in darkness for a long time is not to be put away.

G. K. Noble of the American Museum of Natural History recently met with a similar very interesting case, although he does not interpret it in a Lamarckian sense —that of the American cave Salamander, Typhlotriton (Natural History, Jan.-Feb., 1930), which is blind, with degenerated retina and fused eyelids. Noble was able to breed young individuals both in the dark and in light. Eyes and pigmentation are retained until the time of metamorphosis. Regression takes place after that in natural conditions and in the laboratory in the dark. But if the animals are kept in light the pigmentation persists and the eye remains functional. The facts are of the same order as for Proteus and testify to an instability of the reaction of the organism to external conditions which must be attributed to the cumulative effect of cave life on the ancestors which was induced by the darkness. Something hereditary was acquired, connected with the intrinsic machinery of metamorphosis, which did not exist in the ancestors. It is not a direct and gradual loss as Lamarck imagined it, but a complex and indirect effect, manifesting itself in an unexpected way at the time of metamorphosis.

Such facts, difficult to discover and not very common, seem to me to be an indication of the way changes can be effected. Only in the individual life are direct and limited responses to the external factors of environment evidenced, and they are not directly inherited. Development and differentiation of the individual resides entirely in the mechanism of the intrinsic properties of the egg. But at length, and in an indirect way, this machinery itself can be altered and then responds by changes of equilibrium, most of them being non-adaptive; others, as in the case of the cave animals, adaptive. The exact analysis of such modifications is still to be made and is more or less easy. The final mechanism can be one of

mutations, but the induction of such mutations should be directly ascribed to environment.

My aim was not, as I said, to bring here a solution of these difficult problems, but to put once more in juxtaposition the elements of them and to let you think about them. At the present time, on account of successful development of both genetics and cytology, for which this country has done so much and this laboratory in particular, most biologists are inclined to see in the methods and laws of genetics, in the crude facts of cytology, the whole solution of every biological problem and of all evolution. Certainly we get in this way impressive results. Parallelism of genetical and cytological results is striking and no doubt there is some deep connection with reality. Still, genes are today of conjectural nature, beyond direct testing. Of such problems, the great experimenter, Lavoisier, said very likely "they are susceptible of an infinity of solutions, probably none of which agrees with Nature". One must be very careful when praising beautiful and accurate results not to exclude other explanations because they differ. It seems to me that, in the general sense of today, something like that occurs and we are finally, so far as evolution on a genetical basis goes, confronted with incompatability.

In such a difficult problem as evolution which is our present problem but, more especially, that of the past, we are still at the beginning, even after the great progress made by paleontology, by embryology, and by genetics. We must take into consideration all the facts and aspects of Nature. Adaptation is one of them not to be neglected and to be accounted for, even if the theories at present in favor are difficult to correlate. Such conflicts are, however, frequent in the development of science, and are frequently a condition of progress. We find them in sciences whose domain is much simpler and more exact than biology. It is so, for instance, in physics for the theory of light. At the end of the 17th century Newton built up the emission theory, light being attrib-

uted to the movement of particles at enormous speed; this theory held through the 18th century; it was considered at the beginning of the 19th as real truth, although the explanation of interference and refraction phenomena was quite difficult. Then came Young and Fresnel, who restored the wave theory of Huygens. Fresnel, on this basis, succeeded marvelously in explaining every known optical phenomenon and the theory was able to foresee and explain new ones. The wave theory of light was, during the nineteenth century, one of the finest in all the realm of science, representing perfectly reality. But at the beginning of the present century the theory of the quanta of energy of Planck extended to light reintroduced the considerations of Newton and, some years ago, Louis de Broglie succeeded in reconciling both and associating waves with the movement of electrons.

In an analogous way it seems to me that, as clear and conclusive as the results of embryology, cytology and genetics are, they represent only one particular aspect of the life of organisms, and that, in spite of our failure to show any inheritance of acquired characters, the general Lamarckian conceptions (not the original true theory of Lamarck) cannot be entirely put away; that adaptation is an important and real aspect of living nature, to be explained only by the action of the environmental factors on the organism and by its adaptive response. Evolution cannot be really and totally conceived without it, at least on the basis of natural laws.

We can, however, in science, seize upon but partial aspects of reality and we must not be surprised by such uncertainties as those of biology today. One of the greatest mathematicians of the nineteenth century, lamentably killed at the age of 20 years, Evaniste Galois, expressed that in a very striking sentence: "Science is the work of human mind, whose fate is rather to study than to know, to search for truth than to find it."